

Identifying features in spike trains using binless similarity measures

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Abstract

Neurons in the central nervous system communicate with each other with the help of series of Action Potentials, or spike trains. Various studies have shown that neurons encode information in different features of spike trains, such as the fine temporal structure, mean firing rate, synchrony etc. An important step in understanding the encoding of information by neurons, is to obtain a reliable measure of correlation between different spike trains. In this paper, two new binless similarity measures for spike trains are proposed. The performance of the new measures are compared with some existing measures in their ability to detect important features of spike trains, such as their firing rate, sensitivity to bursts and common periods of silence and detecting synchronous activity.

1 Introduction

The human brain contains around 10^{11} neurons, which form a very large network interconnected with the help of nearly 10^{14} synapses. The neurons are capable of generating an all-or-none impulse of voltage called the Action Potential (AP), which is the fundamental unit of information processing in the nervous system. Series of these action potentials are used by the neurons to communicate with each other. It has been observed that the amplitude and the shape of the action potentials do not vary too much over different trials. Thus it can be assumed that the information is contained mainly in the temporal structure of the spike trains. Single electrode and multi-electrode recordings can be performed to measure these spike trains from single neurons or a population of neurons.

For the analysis of these spike trains, it is often important to quantify the similarity or dissimilarity between two spike trains. This can be required in the study of synchronization of the activity of a population of neurons[1], for studying the reliability of neuronal response when repeatedly presented the same stimulus[2], for testing the discrimination ability of auditory neurons[3], for benchmarking quantitative neuron models[4] etc. Various measures have been proposed for this purpose, such as the Victor-Purpura family of distance metrics[5], the van Rossum distance metric [6], the ISI distance measure [7], the

correlation based similarity measure [8], the Hunter-Milton similarity measure[9] and many more. Comparative studies of these measures have been performed in some recent works such as [10],[11] etc.

From the results and observations of works comparing various similarity measures , such as [10], it can be concluded that there exists no such similarity/distance measure which gives an optimum performance consistently in all the benchmark tests. In particular, taking the examples of the correlation based similarity measure given by Schreiber et al (SC) and the van Rossum distance metric (VR), it was reported that the SC measure performed better than the VR metric in synchrony detection task ,but it wasn't able to give the desired response in mean firing rate detection tests , in which the VR distance metric performed better[10] . Similar observations can be made in the case of other measures also . The performance of a measure is actually governed by the assumptions on which it has been constructed. In this paper we propose two new similarity measures . Our aim is to capture most of the relevant aspects of the neural activity with the help of these two measures . A similar approach was taken in [12] , in which the authors proposed two different similarity measures which were sensitive to bursts and to common periods of silence respectively, and then suggested that a linear combination of the two terms be used as the similarity measure.

The paper is organized as follows: In Sec.2 , the relation between similarity measures and neural code is briefly explained. The existing similarity measures studied in this paper are described in Sec.3 and the new similarity measures are introduced in Sec.4 . A thorough comparison of the performance of different similarity measures is presented in Sec.5 and Sec.6 contains a discussion of the results obtained.

2 Similarity measures and the neural code

Any idea of spike train similarity or dissimilarity is very strongly associated with the concept of neural code. The representation of information in the temporal structure of spike trains of a single neuron , or a population of neurons is called the neural code[13]. In [14] , it has been alternatively defined as the minimum set of neural symbols capable of representing all the biologically relevant information. Neural symbols could be the mean firing rate or some other statistical features of the patterns of spike trains. The term encoding time window is also defined in [14] as the duration of the spike train which corresponds to a single symbol of the neural code. Its limiting value can be obtained by taking the inverse of the maximum frequency with which the neural code is updated to represent dynamic changes in the stimuli . If we take the encoding time window to be N ms long, sampled at the rate of 1kHz , we can represent that segment of a spike train as a binary vector of length N , with '1' present at the points of occurrence of spikes. We can have two limiting cases of the encoding process for the given segment. If we only count the number of spikes occurring in the encoding time window , then all the possible spike train segments can be re-

duced to a single value called the rate of firing. This coding scheme is called the rate coding scheme. On the other extreme if the position of each and every spike is important, we will have a set of 2^N different values corresponding to all the different possible spike train segments. Neural coding requires that the 2^N different possible binary vectors be reduced to a smaller set of neural symbols, or aspects of neural activity which carry the relevant information. In temporal coding it is assumed that not just the number of spikes occurring within the encoding window, but also the pattern of spikes in the window carry significant information.

In this paper we focus mainly on four different aspects of neural activity which might carry important information, namely rate coding, temporal coding and interval coding, and information coding by common periods of silence. In rate coding, it is assumed that within a particular encoding time window, it is only the number of spikes occurring which corresponds to the information about the stimulus. Rate coding is particularly likely in case of neurons where the integration time is larger than the mean Inter Spike Intervals(ISI).[13] As explained in [14], for stimuli with a single time scale, rate coding is only concerned with the number of spikes in the encoding window. If however, the stimulus is dynamic in time, rate coding requires correlation between same frequency components of the stimulus and the corresponding spike train, in the frequency domain. Various methods for estimating the firing rates of spike trains have been discussed in [15]

Temporal coding hypothesis assumes that the relevant information is contained in the precise patterns of the spikes within the encoding window, not just their count. Analogous to the definition of rate coding in frequency domain for dynamic stimuli, requirement for temporal coding as defined in [14], is that there exists some correlation between certain frequency components of the stimuli with higher frequency components of the spike trains. Thus, within the framework of temporal coding, two spike trains which have different times of occurrence of spikes, even though both have equal number of spikes, will be considered different. Alternatively, two neurons which fire synchronously, will be considered to be similar.

Another aspect of information encoding by neurons has been reported in [16], called the interval coding scheme. In that paper, it is reported that the short Inter Spike Intervals(ISIs) that occur during bursts are a distinct feature of the neural code. They have also given an account of some experimental results on pyramidal cells, which when presented with a broadband current injection, responded with bursts, in which the burst ISIs were correlated with the intensity of stimulus upstrokes. It has further been stated that the number of spikes in a burst is also correlated with the slope of the stimulus upstrokes. This encoding of stimulus features in the burst ISIs was termed as interval coding. The role of bursts in information coding has also been studied in some other previous works. In [17], it is reported that bursts encode information in their timing and their durations and that the bursts are much more reliable than isolated spikes, i.e the timing of the bursts are more reproducible across various trials than the timing of isolated spikes. Also the reliability was in direct proportion to the length of

the bursts. In [18], the authors report that although the signalling in many central synapses are very unreliable to individual spikes, the reliability increases considerably to the bursts because of facilitation. Thus those synapses act as a filter, which rejects single spikes while allowing bursts to pass through. Bursts have also been shown to encode information about the direction of movement more reliably than isolated spikes in electrosensory midbrain neurons [19].

Another important feature of neural activity, observed mainly in the Cerebellar Purkinje cells (PC), are the long periods of silence, which are often synchronized over different PCs.[20] The presence of long pauses in the activity of these neurons hints at an inherent bistability in their activity in which the membrane potential transitions between states of continuous firing and periods of quiescence [21]. It has been reported that approximately half of the cerebellar PCs exhibit this behaviour of alternating between long pauses and firing simple spikes [22]. Some experimental studies have shown that the synchronous pauses in firing of converging PCs can induce Deep Cerebellar Nuclei to fire in a reliable fashion [23]. Thus synchronous periods of silence also seem to be a significant aspect of neural code.

In this paper we propose two new measures of spike train similarity. With these two measures we intend to capture all the four different firing properties of neurons discussed above. We also compare the ability of some existing spike train similarity/distance measures in detecting these firing properties.

3 Brief Description of existing measures studied

A large number of measures for spike train similarity and dissimilarity have been proposed, for the purpose of spike train analysis. In this paper, the following spike train similarity / distance measures were studied:-

3.1 Schreiber et al Correlation based similarity measure (SC)

Schreiber et al [8] proposed a new correlation based measure for quantifying the spike timing reliability. This measure is dependent on a single parameter, which is related to the timescale of the precision of spike timing. For calculation of this measure, first the convolution of the two spike trains, represented as a sum of delayed dirac delta functions, is performed with a gaussian kernel, having a standard deviation σ_c . Then the inner product of the two waveforms obtained after smoothing the spike trains is calculated, and normalized with the norms of the individual waveforms, to obtain the measure of similarity. Basically in the discrete time case, if we consider the smoothed spike trains to be vectors in an m dimensional vector space, m being the number of time points, the similarity measure is the cosine of the angle between the two vectors. Thus if the spike trains are represented by s_1 and s_2 and the gaussian kernel with standard deviation σ_c is represented by $G(\sigma_c)$, the similarity measure between s_1 and s_2 can be calculated as

$$x_1 = s_1 * G(\sigma_c) \quad \text{and} \quad x_2 = s_2 * G(\sigma_c) \quad (1)$$

$$S_{corr}(s_1, s_2) = \frac{x_1 \cdot x_2}{|x_1||x_2|} \quad (2)$$

3.2 van Rossum Distance metric(VR)

This distance metric was introduced by van Rossum in [6] . Like the SC measure, this distance also depends on one parameter which defines the timescale considered. For the calculation of this distance measure, first the spike trains are convolved with a decaying exponential signal . As a result of this convolution we get a smooth curve representing the spike train. From the two smooth signals, the distance is calculated as their L^2 norm. The calculations involved are as follows

$$f(t) = \sum_{i=1}^{n_s} u(t - t_i) e^{(t-t_i)/\tau_s} \quad (3)$$

$$D_{VR}(s_1, s_2) = \frac{1}{\tau_s} \int_{t=0}^{\infty} [f_1 - f_2]^2 dt \quad (4)$$

The parameter τ_s determines the time scale over which the influence of a single spike is extended. When the value of this parameter is taken to be very small, the range of influence of each spike is very limited and thus the measure acts as a coincidence detector. In the limiting case of $\tau_s \rightarrow 0$, the distance measure gives the count of non coincident spikes. On the other extreme , with τ tending towards ∞ , the distance measure returns the difference in the total spike count of the two spike trains.

3.3 The Inter Spike Interval(ISI) distance measure

Another spike train distance measure which was proposed in [7] , is the ISI distance measure. This distance measure is different from the other measures, in that it takes into account the inter spike intervals instead of the actual spike occurrence times for the calculation of the distance value. For calculating this distance measure , first a spike train is represented as the set of time of occurrence of spikes, i.e $S = \{t_1, t_2 \dots t_n\}$. To each such spike train, two additional spike times corresponding to the start of the time window , and the end of the time window are added. That is, if the entire duration of the spike train is T ms, then S is modified to include 0 and T as the first and last terms. From this modified spike train , a function f is calculated , such that $f(t) = t_{i+1} - t_i$, for $t_i < t \leq t_{i+1}$. Thus for two spike trains S1 and S2, after obtaining the corresponding f functions , f1 and f2, another function I is calculated in the following way

$$I(t) = 1 - \frac{\min(f1(t), f2(t))}{\max(f1(t), f2(t))} \quad (5)$$

From the function I , the distance between the two spike trains is calculated as

$$D_{ISI}(s1, s2) = \frac{1}{T} \int_{t=0}^T I(t) dt \quad (6)$$

An advantage of the ISI distance measure is that it does not involve any free parameter which has to be selected by the user. However, as a result of this very property, this measure cannot be used to study one particular feature of the encoding of information in the spike train, as it cannot be adjusted to concentrate on a particular aspect of the spike train.

3.4 The Hunter-Milton similarity measure(HM)

Another measure of similarity was proposed in [9], by Hunter and Milton. In this scheme also the spike trains are represented as a set of their occurrence times. For each element in the first spike train (t_{1i}), its nearest neighbour in the second spike train (t_{2i}) is obtained. After getting the nearest neighbour, degree of synchronization or coincidence is obtained by calculating $e^{-\frac{|t_{1i}-t_{2i}|}{\tau_H}}$. These values are then calculated for all the spikes in the first spike train, and their mean is taken to obtain r_{12} . Similarly r_{21} is calculated, by taking the mean of the coincidence values over all the spikes occurring in the second spike train. Finally the similarity measure is the arithmetic mean of r_{12} and r_{21} . Like the SC and the VR measures, the HM measure also has a free parameter τ_H , which determines the range of coincidence of the spikes.

3.5 Lyttle-Fellous similarity measure

In [12], the authors proposed two similarity measures, one sensitive to bursts and the other sensitive to common periods of silence. A convex combination of these two measures could then accordingly be used as a similarity measure, depending upon the situation.

3.5.1 Burst Sensitive measure (LFB)

This measure is a modification of the SC measure. In this measure, the first step involves convolving the spike train with a gaussian kernel of width σ to obtain $f(t)$. A piecewise linear transformation $N(x)$ was applied to each $f(t)$, where $N(x)$ was defined as

$$N(f(t)) = H(f(t) - \eta T)(f(t) - \eta T) \quad (7)$$

Here T is a threshold function which decides which segment of the spike train is considered to be a burst. It depends upon n (minimum number of spikes in a

burst) , b (maximum inter burst ISI) and σ width of the gaussian kernel. The parameter η takes values in the range (0,1) and can be used to set the amount of emphasis to be given to bursts over isolated spikes. T can be calculated by the following expression.

$$T(n, b, \sigma) = \sum_{k=1}^{k=n} e^{\frac{(p-kb)^2}{\sigma^2}} \quad (8)$$

$$p1 = b(n+1)/2 \quad p2 = b(n+2)/2 \quad T = \max(T(p1), T(p2)) \quad (9)$$

The similarity measure is then calculated by taking the standard correlation measure of the $N(f(t))$ of the two spike trains.

3.5.2 Silence Sensetive measure(LFS)

For calculating this measure, the spike trains are mapped to a function($g(t)$) which is set to zero at all the spikes, and then rises linearly in the inter spike interval . The linearly rising part begins after a time delay τ , in order to ignore pauses of smaller lengths. τ can be set to the mean value of all the ISIs , so that only ISI of large durations are considered in this similarity measure. After obtaining $g(t)$ for both the spike trains, the standard correlation measure is calculated for the similarity measure.

4 New similarity measures

In this section , we define the following two similarity measures (SM1 and SM2) :-

The first similarity measure (SM1) is a modified version of the SC measure. In this measure , we first construct a function f from the given spike train . In the case of the SC measure , the function f is obtained by performing the convolution of the spike train with a gaussian kernel of a certain width. Here insted of using a gaussian kernel , we obtain the smoothed signal using the following differential equations.

$$\frac{df(t)}{dt} = -\frac{f(t)}{\tau_f} + S(t).u(t) \quad (10)$$

$$\frac{du(t)}{dt} = -\frac{u(t) - u_0}{\tau_u} + \Delta u.S(t) \quad (11)$$

The function $S(t)$ represents the spike train as a sum of delayed dirac delta functions . The initial value of the variable f is taken to be zero, i.e $f(0) = 0$. If a spike occurs at time t_i , the value of variable f jumps by an amount $u(t_i)$. This is because of the following property of the delta function.

$$\int_{t_i-\epsilon}^{t_i+\epsilon} \delta(t - t_i)dt = 1 \quad (12)$$

Between two spikes, the value of the variable f decays exponentially with a time constant τ_f . This parameter is similar to the corresponding parameters in the VR and SC measures, in the sense that it defines the timescale over which the coincidence of two spikes is considered. The amount by which the variable f jumps with each spike is not constant, it is represented by another variable u . The variable u also jumps at the occurrence of every spike by a fixed value u_0 , and decays exponentially with a time constant τ_u between two spikes. The value of the time constant τ_u is taken to be much smaller than τ_f . This method of generating the variables f and u is quite similar to some simple phenomenological models of facilitating synapses[24]. A similar approach was taken in [25], in which the van Rossum distance measure was studied with a synaptic filter. However, in that paper, the authors reported that they did not get any significant gain in the performance with facilitating synapses. In this paper, our motivation for using a model analogous to that of a facilitating synapse, is to exploit its properties to make the measure more sensitive to bursts. Whenever a spike occurs, the variable f jumps by a value $u(t_-)$, where t_- is the time just before the arrival of the spike. With the arrival of the spike, the variable $u(t)$ also jumps by a value u_0 , i.e $u(t_+) = u(t_-) + \Delta u$. Both the variables then start decaying with their respective time constants. If, however, another spike arrives before u has decayed to a value close to its base value of u_0 , the next jump in f would be higher than the previous jump. This kind of situation occurs in the case of bursts, where a group of spikes occur with very small interspike intervals. Thus if the value of the time constant τ_u is comparable to the interspike intervals, the variable f will rise considerably during the occurrence of the bursts, and if the bursts occur simultaneously in two spike trains, it will be reflected in the higher value of the similarity measure.

An important distance measure used in information theory is the Hamming distance, which calculates the distance between two vectors as the number of positions at which they differ. Alternatively it counts the minimum number of changes to be made to transform one vector to the other. It is not feasible to directly apply the Hamming distance to the binary representation of two spike trains, as it would consider two coinciding spikes as no different from two points from interspike intervals. For the second distance measure (SM2), we use the basic idea of the Hamming distance and modify it to make it more suitable for application to spike trains.

Given two spike trains $S1$ and $S2$, we first obtain their smoothed versions by convolving them with a suitable smoothing kernel. We have used the decaying exponential kernel in this paper, but other kernels can also be applied. Let the smoothed spike trains be $r1(t)$ and $r2(t)$. Then the similarity measure (SM2) is calculated as follows:

$$d2(S1, S2) = \frac{1}{T} \int_{t=0}^T x(t) dt \quad (13)$$

$$SM2(S1, S2) = 1 - d2 \quad (14)$$

where x is defined as

$$x(t) = \begin{cases} 1, & \min(r1(t), r2(t)) \leq k * \max(r1(t), r2(t)) \\ 0, & \text{otherwise} \end{cases}$$

Here two points of $r1(t)$ and $r2(t)$ are taken to be similar if the smaller of the two values is greater than k times the larger. The parameter $k \in (0,1)$, and it denotes the amount of tolerance allowed for two points of $r1(t)$ and $r2(t)$ to be considered similar. A typical value we used in our simulations was 0.7. Using this definition, the distance $d2$ is calculated for $r1$ and $r2$, and $1 - d2$ is defined as the similarity measure.

5 Performance tests of the similarity measures.

In this section, we compare the performance of all the different similarity measures discussed so far in the paper. We will be comparing the performance of the measures in the following

- Firing rate discrimination
- Burst Sensitivity
- Sensitivity to common periods of silence
- Synchronous firing detection

These tests correspond to the different aspects of neural coding that we discussed in Section 2.

5.1 Firing rate discrimination

To study the firing rate discrimination ability of the measures we first used a test similar to the one described in [10]. For the test, we generated artificial spike trains, each 5s long, using a homogenous poisson process[26]. The mean firing rate of one spike train was kept fixed at 20 Hz, while the firing rate of the second spike train was varied from 2Hz to 40 Hz in steps of 2. For each combination of firing rates, 100 pairs of spike trains were generated, and the entire process was repeated for 1000 times. The parameters used are shown in Table 1.

Figure 1 shows the performance of the similarity measures. If a similarity measure has the ability to detect differences in the mean firing rate of two spike trains, then the similarity values should be maximum for the rate of 20Hz, and it should decrease as we move away from 20 Hz on both sides. For plotting all the measures on the same graph, we had to modify some of the measures. The ISI was converted into a similarity measure by taking $S_{ISI} = 1 - D_{ISI}$. The maximum mean value of the van Rossum distance measure over all the trials was around 364. So, for showing it on the same plot, we converted it into a similarity measure by defining $S_{VR} = 1 - D_{VR}/450$. The performance of SM1,

Similarity Measure	Parameter Values used
SM1	$\tau_f=100\text{ms}$, $\tau_u=5\text{ms}$, $u_0=0.3$, $\Delta u=0.2$
SM2	$\tau=100$ ms , $k = 0.7$
SC	$\sigma_c = 100$ ms
VR	$\tau_s = 100$ ms
HM	$\tau_H=100$ ms
ISI	-

Table 1: Various parameter values used in the firing rate test

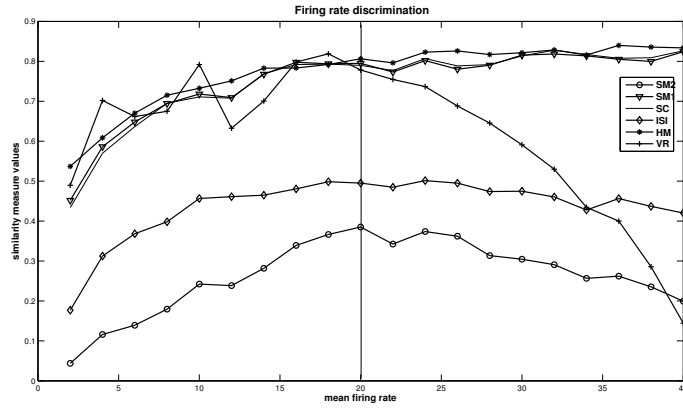


Figure 1: The figure shows the performance of the six similarity measures , in the test for firing rate difference discrimination. The VR and SM2 were the two best performers in this test.

SC and HM measures are almost identical. They show the correct behaviour when the firing rate of the second spike train is below the reference firing rate(20 Hz) . However for higher firing rates, the similarity measure values either stay almost constant or go up instead of decreasing. The two best performing measures were the VR and SM2 measures.

To further study the ability of the similarity measures to classify spike trains based on their mean firing rates , we generated 8 sets of spike trains of 5s length with mean firing rates varying from 5Hz to 40 Hz , with each set containing 50 spike trains. We used the classification scheme suggested in [5] . A confusion matrix $N(r_i, r_j)$ was constructed using the various similarity/distance measures. $N(r_i, r_j)$ represents the number of times a spike train of mean firing rate r_i has been classified in the set corresponding to mean firing rate r_j . The confusion matrix is initialized as a null matrix of dimension $N_s \times N_s$ (N_s =number of sets=8) . For each spike train s, its mean distance from the spike trains of the

Distance/Similarity Measure	H/H_{max}
SC	0.045
VR	0.426
ISI	0.334
SM1	0.035
SM2	0.375
HM	0.0267
LFB	0.021
LFS	0.142

Table 2: The performance of the different measures in clustering the spike trains on the basis of their mean firing rates are shown in the table. The H values have been normalized by H_{max} , which corresponds to the case of perfect clustering.

different sets is calculated according to the following formula.

$$d(s, r_i) = \left[\left\langle (d(s, s_{r_i}))^z \right\rangle \right]^{\frac{1}{z}} \quad (15)$$

Here $d(s, s_{r_i})$ is the distance between the spike train under consideration s , and a spike train from the set with mean firing rate r_i . The given spike train s is allotted to the set, with which it gives the minimum value of the mean distance. Using this process the confusion matrix is completed. For an ideal classifier the confusion matrix N would be a diagonal matrix. To quantify the performance of the classification, we used the information theoretic measure, transmitted information (H) [5]. We normalized the values of H by its maximum value H_{max} , which is given by $H_{max} = \log_2(N_s)$ corresponding to the case of perfect classification, where N_s is the number of sets in which the data is to be classified. The values of normalized H are listed in the Table 2

From the Table 2, we can see that the VR measure performed the best in classifying spike trains based on their mean firing rates, followed by the SM2 and ISI measures. All the similarity measures which involved calculating inner products performed poorly in this test.

5.2 Burst Sensitivity

Bursts are a very important component of neural signalling, as they are known to increase the reliability of synapses in the central nervous system. Many synapses transmit bursts but do not respond to single spikes, thus acting as a filter [18]. To test the sensitivity of similarity measures to bursts, we will follow a procedure similar to the one used in [12]. We first generated two poisson spike trains, 5 seconds long, with mean firing rates of 20 spks/sec and 30 spks/sec respectively. The similarity/distance measures were calculated for these two spike trains. Then, the two spike trains were modified by adding some bursts at same positions and deleting an equivalent number of isolated spikes.

N_{bursts}	ISI	VR	SC	HM	LFS	LFB	SM2	SM1
3	1.019	0.998	1.309	1.146	1.014	1.9544($\eta=0.5$)	1.132	1.523
6	1.038	0.996	1.541	1.274	1.019	2.940($\eta=0.5$)	1.266	1.881

Table 3: The S_B values obtained for the different measures in the two cases are shown in the table

The similarity /distance measures were again calculated for the modified spike trains. This process was repeated for 1000 times. For a similarity (distance) measure sensitive to bursts, the value should be higher (lower) in the case of the modified spike trains. To quantify the sensitivity of the measures to bursts of action potential , the following term was calculated

$$S_B = \frac{1}{n} \sum_{i=1}^{i=n} \frac{Sim(s1^*, s2^*)}{Sim(s1, s2)} \quad (16)$$

Here Sim denotes any similarity measure and n is the total number of trials. s1 and s2 are the original spike trains, whereas $s1^*$ and $s2^*$ represent the modified spike trains. In the case of VR measure , the ratio was inverted , while the ISI measure was changed into a similarity measure, by taking its difference from unity. Thus for a measure which emphasizes bursts of action potentials more than isolated spikes, the value of S_B should be greater than one. Table 3 shows the values of S_B obtained for various measures.

The LFB measure and the SM1 measures were the most versatile measures , with regards to burst sensitivity. The parameter η in LFB , and u_0 and Δu in SM1 can be tuned to adjust the emphasis to be given to the bursts. The S_B value for SM1 in the table correspond to the values of $(u_0, \Delta u) = (0.2, 0.4)$. By increasing Δu and reducing u_0 (or keeping it constant) , the weightage given to bursts can be increased. So when $(u_0, \Delta u)$ were changed to $(0.1, 0.5)$, the S_B values of SM1 increased to 1.887 and 2.43 with the addition of 3 and 6 bursts respectively. Other measures which performed well in this test were SC , HM and SM2 . In the case of LFS, ISI and VR , the introduction of bursts did not seem to have much effect on the similarity/distance measure values.

5.3 Sensitivity to common periods of silence

Common periods of quiescence have also been suggested as an important aspect of information coding , especially in the case of cerebellar micorcircuits. To test the sensitivity of measures to common periods of silence , we followed the following procedure . Two poisson spike trains of length 5ms each, were generated and the similarity/distance values between them were obtained. The two spike trains were modified to include a period of silence of length L_s at the same position , and the similarity/distance values were calculated for these two trains. The value of L_s was varied from 100 ms to 500 ms, and the entire process was repeated 1000 times. The sensitivity was quantified using a term S_S , defined in a similar way to S_B .

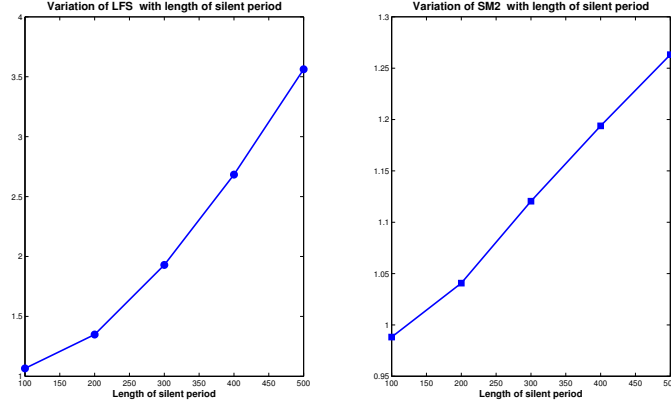


Figure 2: LFS and SM2 the only measures which displayed any significant variation with the introduction of a silent segment. LFS has been specially constructed to be responsive to silent periods, and it showed very large variation with the length of segment inserted. SM2 varied almost linearly with the length of silent period, although the slope of variation was quite small as compared to LFS

It was observed that the insertion of common silent periods had negligible effect in the case of all the measures except LFS and SM2. LFS was the most responsive to the introduction of common periods of silence, with its S_S values increasing rapidly with increasing length of the segment introduced. SM2 showed an almost linear variation with increasing length of the silent segment embedded, although the rate of increase was much smaller than in the case of LFS.

5.4 Synchronous firing detection

Synchronous neural activity is an important component of information processing in the brain. It has been hypothesized to be involved in information encoding, influencing transmission of activity from one group of neurons to another, facilitating a group of neurons with common post synaptic targets to depolarize them more effectively.[13]. Here, by synchronous spike trains, we mean spike trains in which the timings of spikes are correlated.

For studying the ability of measures to detect synchronous firing, we generated the dataset using a procedure resembling those used in [8] and [10]. First a reference poisson spike train with mean firing rate of 20 spks/sec was generated. From this reference spike train, new spike trains were generated using the following procedure:-

- Each spike of the reference spike train was considered individually. Any spike of the reference spike train was retained in the new spike train with

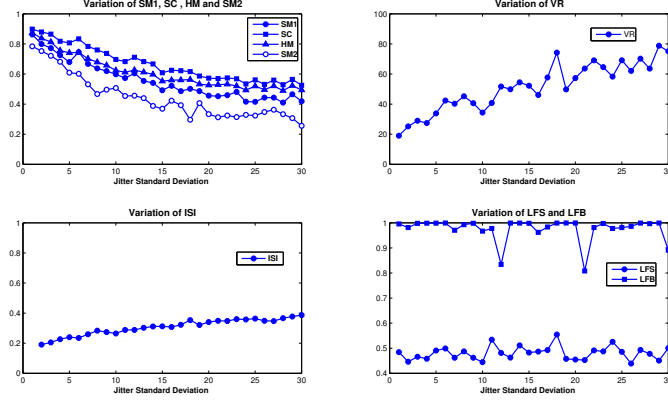


Figure 3: The figure shows how the different measures responded to change in the values of jitter in spike timing. All the measures except LFS and LFB followed the expected trend of decreasing similarity with increasing jitter in spike timing.

a probability p_r . The term p_r reflects the reliability of the data. A high value of p_r (i.e close to 1) corresponds to greater reliability.

- The time of occurrence of the spikes of the reference spike train was carried over into the new spike train with some jitter. The amount of jitter was taken randomly from a gaussian distribution with a standard deviation of σ_j . The term σ_j represents the precision in the timing of the spikes over different trials. Smaller σ_j means greater precision in spike timing.
- To represent background activity, the spike train obtained after the previous two steps was superimposed with a background spike train, with mean firing rate r_b . The value of r_b was taken to be much smaller than the mean firing rate of the reference spike train.

The values of σ_j was varied in the range (1, 30) ms in steps of 1, while p_r ranged from 0.40 to 0.98 in steps of 0.02. r_b was kept fixed at 5 spks/sec. For each combination of (σ_j, p_r) , $ns = 50$ spike trains were generated. In this way a large number (30*30*50) of spike trains were generated, and the behaviour of the different measures were studied on this data set.

In Figure 3, the variation of the different measure values for a fixed p_r (0.8) and varying σ_j is shown. As the σ_j value increases, the precision of spike timing over different trials decreases. So it is expected that the similarity(distance) values should decrease (increase) with increasing σ_j . This general trend is followed by all the different measures except LFS and LFB.

Figure 4 shows how the different measures vary with σ_j kept fixed (10 ms), and varying p_r . As the value of p_r is increased, the reliability of the spikes

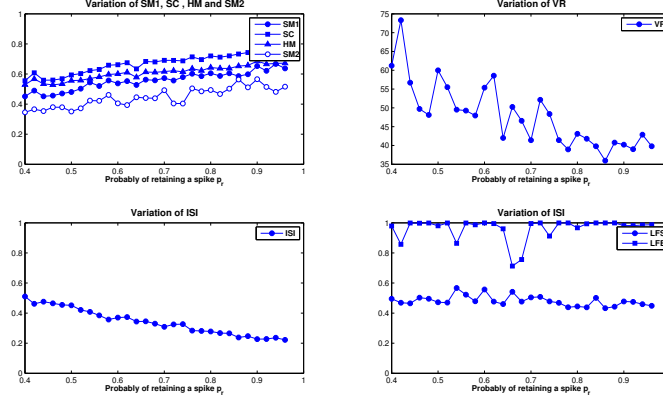


Figure 4: The figure shows the variation of the different measures , with increasing reliability of spikes . All the measures except LFS and LFB followed the expected trend.

Set No.	σ_j (ms)	p_r	r_b (spks/sec)
Set 1	(12,20)	(0.85,1)	(6,9)
Set 2	(6,12)	(0.70,0.85)	(3,6)
Set 3	(0,6)	(0.55,0.70)	(0,3)

Table 4: The table shows the range of values of the three parameters used for creating three different sets of spike trains.

over different trials increases . Thus the values of similarity (distance) measures should increase (decrease) with increasing probability of retention of spikes . SC , SM1 ,SM3 , HM and ISI measures showed the desired variation with increasing values of p_r . Although the VR measure generally followed the desired trend, it also showed large fluctuations. In this case also the LFS and LFB failed to respond in the expected manner.

To further study the ability of the different measures to detect synchrony , they were used in the following classification problem . First a reference poisson spike train with a mean firing rate of r_0 was generated. From this reference spike train , three different sets of spike trains with different ranges of the three parameters σ_j , p_r and r_b were obtained. The values of these parameters used are given in Table 3 . 100 spike trains for each set were genrated by randomly selecting the different parameters from the ranges shown in the table. The first set corresponds to spike trains with high reliability , but low precision in spike times and high background activity . The third set contains spike trains with low reliability , but high precision and small amount of background activity. In the second set , moderate values of reliability , precision and background noise are used. The same clustering scheme , which was used in classifying spike trains

Table 5: The performance of the different measures in the clustering problem , at low mean firing rate ($r_0=15$ spks/sec) . The SM1 showed the best performance in this case.

Similarity/Distance Measure	H/H_{max}
SM1	0.455
VR	0.118
SC	0.392
SM2	0.147
HM	0.386
ISI	0.352
LFB	0.246
LFS	0.064

Similarity/Distance Measure	H/H_{max}
SM1	0.516
VR	0.327
SC	0.557
SM2	0.598
HM	0.4536
ISI	0.1325
LFB	0.367
LFS	0.148

Table 6: The table lists the performance index for the different measures in clustering the spike trains, when the mean firing rate of the reference spike train was high(50 spks/sec). In this case the best performing measure was SM2 , closely followed by SC and SM1.

based on their mean firing rates , is used here too. Two different values of the mean firing rate of the reference spike train (15 spks/sec and 50 spks/sec) were used corresponding to low and high values of mean firing rate. The results of the two clustering problems are shown in Table4 and Table 5. Some measures like SM1 , SC and HM performed well in the classification task at both, high as well as low mean firing rates , while SM2 , LFB and VR worked better in the case of spike trains with higher firing rate. ISI measure on the other hand , performed better with $r_0 = 15$.

6 Discussion

In this paper, we have introduced two new measures for quantifying similarity between a pair of spike trains. The first of these measures (SM1) is a modification of an existing correlation based measure (SC) proposed in [8] . Here , instead of using a gaussian kernel for smoothing the spike trains, we have em-

ployed a process which is similar to that used in obtaining the post synaptic trace in phenomenological models of facilitating synapses. Thus, in general this measure exhibits behaviour quite similar to that of the SC measure, but has an added feature of being burst sensitive. The burst sensitivity of this new measure can be tuned according to the requirements, by varying the parameters u_0 and Δu . Like the SC measure, this new measure also did not perform well in classifying spike trains based on their mean firing rates. However, using this measure, very good classification of spike trains based on synchrony was obtained.

The second similarity measure(SM2) introduced in this paper, has been motivated from the well known distance measure used in information theory, called the Hamming distance. Hamming distance between two vectors is the number of positions at which the two vectors differ. In case of spike trains, two coincident action potentials are a much more significant event than two points on the silent parts of the spike trains. However, these two occurrences will be treated equally in calculating Hamming distance, and hence it cannot be directly applied to spike trains. So, for calculating SM2, we first smoothed out the spike trains with an exponential kernel. Then two corresponding points of the smoothed spike trains were defined to be equal, if the absolute value of their difference is less than $(1-k)$ times the greater of the two values. Using this definition, the modified Hamming distance (d_2) was calculated, and SM2 was obtained by subtracting d_2 from 1. This measure performed well in the classification of spike trains based on their mean firing rate, as well as in the classification of spike trains based on synchronous firing, when the mean firing rate of the reference spike train was high(50 spks/sec). SM2 was also the only measure, other than LFS, which was sensitive to common pauses introduced in the spike trains. However, unlike the LFS measure, it also performed well in other tests.

We compared the performance of the two new measures, with some existing measures on their ability to detect important features of spike trains, such as their firing rate, sensitivity to bursts and common periods of silence and detecting synchronous activity. SM1 showed the ability to emphasize bursts over isolated spikes, and also performed well in detecting synchronous firing. SM2, on the other hand, performed well in classification based on firing rate, and also exhibited sensitivity to common periods of silence. SM2 was also able to outperform other measures in classifying the spike trains at higher mean firing rate. In this way, these two measures can be used to identify all the four important characteristics of spike trains mentioned above.

In future, work can be done to develop new spike train clustering techniques which utilizes both the new similarity measures proposed in this paper. Such a clustering technique could benefit from the complementary advantages of the two measures, and provide optimum classification of spike trains.

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